
A PHYLOGENETIC CONSPECTUS OF THE TRIBE JUANULLOEAE (SOLANACEAE)¹

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ABSTRACT

The tribe Juanulloeae has traditionally consisted of nine genera of rarely collected, epiphytic shrubs and small trees: *Juanulloa*, *Markea*, *Schultesianthus*, *Trianaea*, *Dyssochroma*, *Hawkesiophyton*, *Rahowardiana*, *Ectozoma*, and *Merinthopodium*. Here we present the results of a cladistic study of the relationships of the species of these genera and provide a conspectus of the genera as we define them. The number of genera in our treatment is reduced to six: *Dyssochroma*, *Juanulloa*, *Markea*, *Merinthopodium*, *Schultesianthus*, and *Trianaea*. Included in the key and conspectus is the genus *Solandra*, which at present is treated as a separate tribe, Solandreae. We also discuss the groupings on the tree and point out areas for future research in this group. A key to the genera is provided and for each genus a list of component taxa and their distributions is also given. Many of these genera have previously been illustrated, but illustrations are provided for some of the previously unillustrated taxa or for taxa where illustrations are difficult to find.

The Solanaceae are an economically important, cosmopolitan family with over 2500 species that have traditionally been divided into two subfamilies. The Cestroideae, including petunias, the cestrums and their relatives, have non-compressed, often prismatic seeds and tropane alkaloids. The Solanoideae, which contain the large majority of the species in the family, include *Solanum* and its relatives that have compressed seeds and steroidal alkaloids. This traditional classification has recently been challenged by cladistic analyses using chloroplast and nuclear DNA data sets, and the family can now be divided into approximately seven monophyletic groups (see Olmstead et al., in press).

The tribe Juanulloeae, first described by Hunziker (1977), is placed in the subfamily Solanoideae in both the traditional and phylogenetic systems: its members share flat, discoidal seeds and curved embryos with others in that subfamily. The tribe as defined by Hunziker (1977, 1979) is delimited by a combination of habit, anther, and seed characters and consists of nine genera: *Dyssochroma* Miers, *Ectozoma* Miers, *Hawkesiophyton* Hunz., *Juanulloa* Ruiz & Pavón, *Merinthopodium* Donn. Sm., *Markea* Rich., *Rahowardiana* D'Arcy, *Schultesianthus* Hunz., and *Trianaea* Planch. & Linden. The Juanulloeae are thought to be closely related to the genus *Solandra* Swartz, the only member of the So-

landreae. *Trianaea* was previously considered a member of the Solandreae (Hunziker, 1979; Bernardello & Hunziker, 1987), but was transferred to the Juanulloeae (Hunziker & Bernardello, 1989) owing to its ex-endospermous seeds and almost straight embryos with oblique, accumbent cotyledons. *Solandra* differs from the members of the Juanulloeae in its incumbent rather than accumbent cotyledons and its partially inferior ovary (D'Arcy, 1973 [1974]). Miers (1857) allied *Solandra*, *Juanulloa*, *Markea*, *Sarcophysa* Miers (*Juanulloa speciosa* (Miers) Dunal), and *Dyssochroma* as the Solandreae, which he considered to be closely related to the shrubby neotropical genus *Brunfelsia* L. *Brunfelsia* is now considered to be related either to *Salpiglossis* L. and its relatives (Hunziker, 1979) or to *Petunia* L. (Olmstead et al., in press). In the recent molecular phylogeny of the family Juanulloinae and Solandrinae are united in the tribe Juanulloeae (see Olmstead et al., in press). The general habit and morphological similarities of the Juanulloeae and *Solandra* have long been recognized and we have thus included *Solandra* in this analysis.

The genera of the Juanulloeae (here referred to in the broad sense, including *Solandra*) are all neotropical, epiphytic trees and shrubs. Many of the species are myrmecophilous, especially in the ge-

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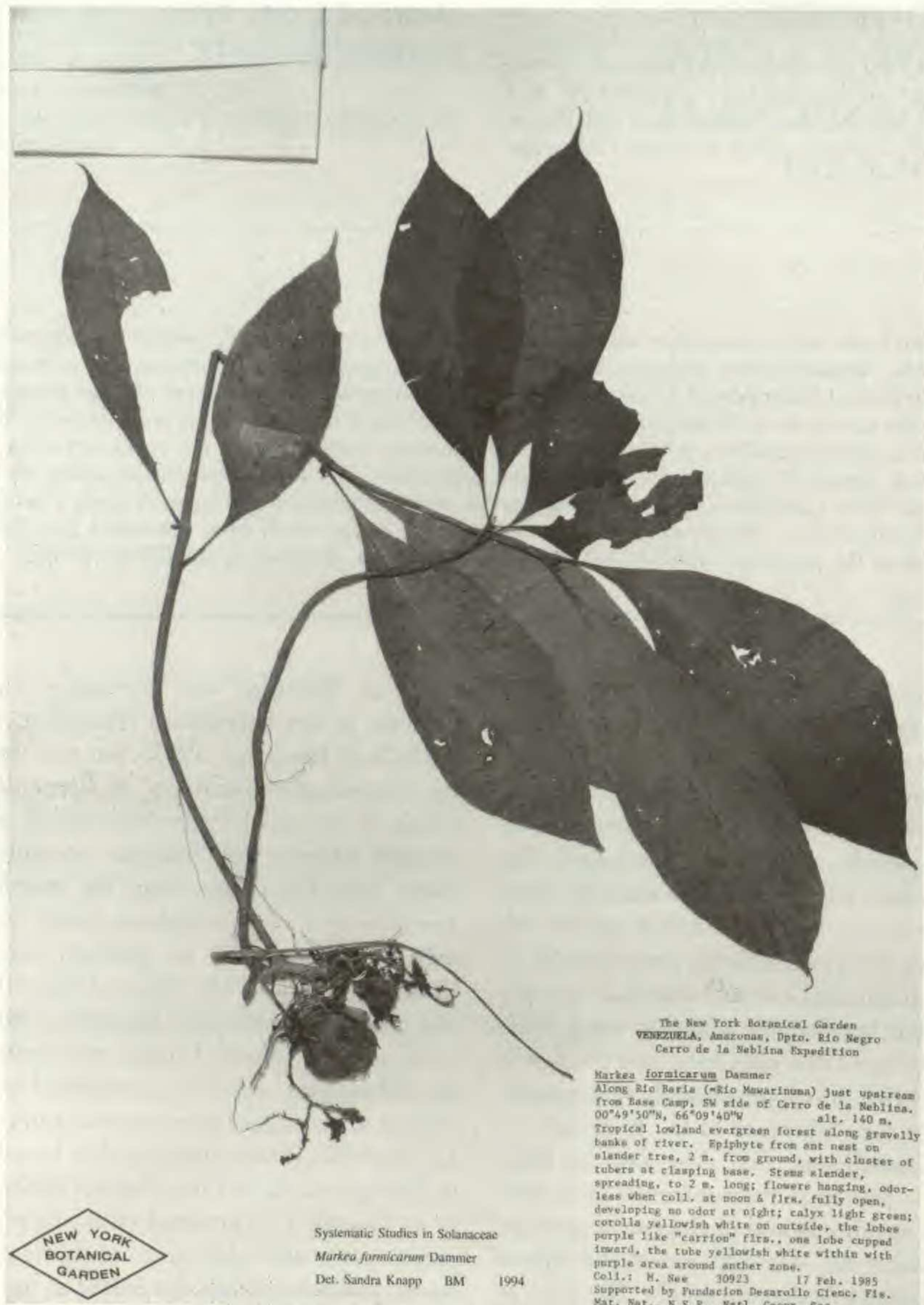


Figure 1. *Markea formicarum* Dammer. Specimen illustrating the swollen ant-inhabited stem-bases (See 30923, NY).

nus *Markea*, where two Amazonian species are associated with particular species of ants (Ducke, 1915: *M. camponoti* Ducke associated with *Camponotus femoratus* (F.) and *M. formicarum* Damm. with *Azteca* sp.). Species of *Hawkesiophyton* (here treated as congeneric with *Markea*) are often associated with various species of ants (Ducke, 1922), and seedlings of *M. panamense* Standl. produce enlarged basal stems even in the absence of ants (Garwood, pers. comm.). The swollen tuber-like stems and roots seen in these species (Fig. 1) are often hollow and are probably used by ants for

nests and storage. In some ant plants, a mutualistic relationship exists between the insect and the plant, with high percentages of both carbon and nitrogen being derived from ant respiration and debris deposition (Treseder et al., 1995).

Some members of the Juanulloeae are fed upon by the larvae of the Ithomiinae (Lepidoptera: Nymphalidae), specialist herbivores of the family Solanaceae. *Solandra*, *Schultesianthus*, *Markea*, *Juanulloa*, and *Merinthopodium* are fed upon by larvae of the genera *Olyras*, *Eutresis*, and *Melinaea* (tribe Melinaeini), which are all high flying canopy dwell-



Figure 2. —A. *Juanulloa mexicana* (Schltdl.) Miers, cult. Royal Botanic Gardens, Kew, scale bar = 1.5 cm.—B. *Solandra maxima* Sessé & Mociño, cultivated, University of Texas, Austin, TX, originally collected at Las Tuxtlas, Veracruz, Mexico (photo J. Mallet), scale bar = 4 cm.



Figure 3. —A. *Merinthopodium neuranthum* (Hemsl.) Donn. Sm., fallen flower post-anthesis; note the broadly campanulate shape (Monteverde, Costa Rica), scale bar = 2 cm.—B. *Trianaea speciosa* (Drake) Soler., Knapp et al. 9121, Loja-Zamora road, Ecuador, scale bar = 2 cm.

ers (for a complete listing of the host plant relationships of these butterflies see Drummond & Brown, 1987). The young larvae make characteristic "C"-shaped damage in the leaves, but have rarely been reared and are difficult to collect from the forest canopy.

In common with many other tropical epiphytes the leaves of species in the group tend to be thick and leathery, and the branches flexible with pliable bark. Flower shape in the Juanulloeae varies considerably from the long, red or bright orange, presumably hummingbird-pollinated, flowers of *Markea coccinea* Rich. and most of the species of *Juanulloa* (Fig. 2A) to the greenish, open campanulate flowers of the species of *Trianaea* (Fig. 3B), *Merinthopodium* (Fig. 3A), and *Dyssochroma*, which are bat-pollinated (Voss et al., 1980). In every case, apart from *Markea panamensis*, however, the flowers are sympetalous and have relatively long corolla tubes. Fruits of members of the Juanulloeae are generally fleshy to leathery berries, with some variation in the thickness of the berry wall. Genera of

the tribe have been traditionally delimited (Hunziker, 1977, 1979) using combinations of the following characters: insertion of the anthers on the filaments, filament insertion on the corolla tube, and corolla aestivation. Characters and their states are discussed more fully in Materials and Methods.

Few collections are known for most of the species and this makes the assessment of characters difficult since the extent of variability is not known. Woody tropical epiphytes are difficult to collect as they often grow high in the canopy and flower only rarely. Many of the species of the Juanulloeae are known only from flowering material, and thus decisions based on fruit characters tend to be rather ad hoc at best. With few specimens available it is nearly impossible to assess variability in characters, and a tendency to overdivide at the generic level is apparent and understandable.

Recent applications of molecular systematics have been extremely useful in providing broad frameworks for directing future study. However, at present, the limited range of taxa that has been

Table 1. Taxa used in the cladistic analysis. Names in parentheses are those used in Persson et al. (1994).

<i>Nicandra physalodes</i> (L.) Gaertner
<i>Atropa belladonna</i> L.
<i>Lycium cestroides</i> Schltldl.
<i>Dyssochroma longipes</i> (Sendtner) Miers
<i>Dyssochroma viridiflora</i> (Sims) Miers
<i>Juanulloa ferruginea</i> Cuatrecasas
<i>Juanulloa globifera</i> (S. Knapp & D'Arcy) S. Knapp (<i>Rahowardiana globifera</i>)
<i>Juanulloa membranacea</i> Rusby
<i>Juanulloa mexicana</i> (Schltldl.) Miers
<i>Juanulloa ochracea</i> Cuatrecasas
<i>Juanulloa parasitica</i> Ruiz & Pavón
<i>Juanulloa parviflora</i> (Ducke) Cuatrecasas
<i>Juanulloa pavonii</i> (Miers) Benth. & Hook. (<i>Ectozoma pavonii</i>)
<i>Juanulloa speciosa</i> (Miers) Dunal
<i>Juanulloa verrucosa</i> (Rusby) Hunz.
<i>Juanulloa wardiana</i> (D'Arcy) S. Knapp (<i>Rahowardiana wardiana</i>)
<i>Markea camponoti</i> Ducke
<i>Markea coccinea</i> Rich.
<i>Markea costanensis</i> Steyerm.
<i>Markea formicarum</i> Ducke
<i>Markea panamensis</i> Standl. (<i>Hawkesiophyton panamense</i>)
<i>Markea sessiliflora</i> Ducke
<i>Markea ulei</i> (Dammer) Cuatr. (<i>Hawkesiophyton ulei</i>)
<i>Markea lopezii</i> Hunz.
<i>Markea</i> aff. <i>lopezii</i>
<i>Merinthopodium neuranthum</i> (Hemsl.) Donn. Sm.
<i>Merinthopodium pendulum</i> (Cuatr.) Hunz.
<i>Schultesianthus coriaceus</i> (Kuntze) Hunz.
<i>Schultesianthus crosbianus</i> (D'Arcy) S. Knapp (<i>Markea crosbiana</i>)
<i>Schultesianthus dudleyi</i> Bernardello & Hunz.
<i>Schultesianthus leucanthus</i> (Donn. Sm.) Hunz.
<i>Schultesianthus megalandrus</i> (Dunal) Hunz.
<i>Schultesianthus odoriferus</i> (Cuatr.) Hunz.
<i>Schultesianthus uniflorus</i> (Lundell) S. Knapp (<i>Markea uniflora</i>)
<i>Schultesianthus venosus</i> (Standl. & C. V. Morton) S. Knapp (<i>Markea venosa</i>)
<i>Solandra brachycalyx</i> Kuntze
<i>Solandra boliviana</i> Britton
<i>Trianaea brevipes</i> (Cuatr.) S. Knapp (<i>Trianaea spectabilis</i> var. <i>brevipes</i>)
<i>Trianaea naeka</i> S. Knapp (<i>Trianaea</i> sp. 1)
<i>Trianaea neovisae</i> Romero-Castañeda
<i>Trianaea nobilis</i> Planch. & Linden
<i>Trianaea speciosa</i> (Drake) Soler.
<i>Trianaea</i> sp. nov. (<i>Trianaea</i> sp. 4)

ily level, and thus relationships are more resolved. This is certainly true for this analysis of the Juanulloae. The molecular analyses of Solanaceae undertaken to date have indicated a close relationship among *Juanulloa*, *Dyssochroma*, *Hawkesiophyton* (= *Markea*), and *Solandra* (Olmstead & Palmer, 1992; Olmstead & Sweere, 1994; Olmstead et al., in press). However, in those analyses only four species were sampled, thus somewhat limiting their usefulness at resolving relationships among genera or in determining whether or not the genera as presently defined are monophyletic.

This paper presents a cladistic analysis of the Juanulloae based on macro- and micromorphological characters. It extends an earlier analysis that emphasized palynological characters (Persson et al., 1994) and provides a conspectus of the genera and species.

MATERIALS AND METHODS

Taxa used in the cladistic analysis are listed in Table 1. By using species as terminal taxa we hoped to test the monophyly of genera in the group as presently defined. Nomenclatural changes necessitated by the results of this study were made in Knapp (1995), and the new combinations are used here. The names used in Persson et al. (1994) did not reflect these nomenclatural changes and thus are slightly different. Names in parentheses in Table 1 are those used in Persson et al. (1994) when a new combination is used here. Morphological characters were assessed using herbarium specimens from BM, CUVC, F, JAUM, K, MO, NY, and QCNE, and voucher specimens are cited in the appendix. Palynological characters were assessed as described in Persson et al. (1994), and pollen slides have been deposited in the collections at BM.

The cladistic analyses were performed using the computer program Hennig86 (Farris, 1988) using the *mhennig** option for the initial selection of most parsimonious trees, then *bb** for finding equally parsimonious trees. These options are recommended for use with large data sets where exhaustive iteration can be prohibitively time-consuming for finding shortest trees (Farris, 1988), and have been shown to be as good as the *ie* option in many test data sets (Platnick, 1989). The ensemble consistency index (CI) is a measure of homoplasy in the data set with respect to the fit of characters to the tree. When the fit of a character is perfect (with no parallelism or reversal) then the consistency index equals 1. The ensemble retention index (RI) is the fraction of apparent synapomorphy in a character that is retained as synapomorphy on the tree (Far-

sampled makes direct comparison of these results to those from morphological studies difficult. The sampling of morphological characters is often more complete in any given group, especially at the fam-

ris, 1989). Trees were also constructed using NONA (Goloboff, 1993) to confirm the actual versus potential groupings on the tree, as NONA and Hennig86 treat zero length branches (potential groupings) in a different way. The following commands, as recommended by Goloboff (1993), were used: hold 100, hold/20, and mult*50.

Successive approximation weighting (*xs w* option in Hennig86) was used to assess the reliability of fit of characters to the most parsimonious tree. The fitting function in the MS-DOS program PeeWee (Goloboff, 1993) was also used to assess character reliability. Character weighting, when applied to the fit of characters, emphasizes those characters that best fit the initial tree topology. Successive weighting allows the characters to judge themselves in terms of their reliability: i.e., their best fit to the solution supported by all the data (Carpenter, 1994). Best fit is judged by the shortest tree (Farris et al., 1970), the shortest tree for the weighted data in terms of tree length (Farris, 1969), or the "heaviest" tree when calculated as a function of character weights (Goloboff, 1993). Characters that are more homoplasious are less reliable and are thus downweighted in these analyses. Successive weighting (Hennig86, *xs w* option) uses the rescaled consistency index (*rc*) of Farris (1989) as the weighting function of each character: it is calculated as the product of ensemble RI (retention index) times ensemble CI (consistency index) and scaled between 0 and 10. Goloboff (1993) calculates weights as the extra number of steps per character such that the weight = $K/K+ESi$, where *ESi* is the extra steps per character and *K* is the concavity constant (in our analyses set at *K* = 3).

The characters were coded to be unordered, thus minimizing ad hoc weighting or polarity before analysis. In this analysis we used 43 taxa and 38 characters (Table 2). Three taxa were selected as outgroups (see Tables 1 and 3), *Nicandra physalodes*, *Atropa belladonna*, and *Lycium cestroides*, representing a range of putative sister taxa for the Juanulloeae. Choosing a range of outgroups (Watrous & Wheeler, 1981) has been thought to increase the likelihood of obtaining an accurately rooted tree. Recent work, however (Nixon & Carpenter, 1993), has shown that multiple outgroups perform no better at "polarizing" ingroup nodes, but that multiple outgroups might improve inference. One difference in this data set from that used in Persson et al. (1994) is the omission of *Mandragora* as one of the outgroups for the analysis. Olmstead and Palmer (1992) had originally identified *Mandragora* and *Solandra* as sister taxa using chloroplast DNA restriction site mapping. More recent work has revealed that *Mandragora* is an isolated taxon of uncertain affinity, possessing many autoapomor-

Table 2. Characters used in the cladistic analysis of the Juanulloeae.

0.	Habit shrubs 0, herbs 1, epiphytes 2.
1.	Peltate glandular trichomes on leaf surfaces absent 0, present 1.
2.	Inflorescence of solitary flowers 1, few flowers 0, many flowers 2.
3.	Inflorescence axis condensed 0, elongate 1.
4.	Calyx lobes shorter than the corolla tube 0, equal to the corolla tube 1.
5.	Calyx texture at anthesis membranous 0, coriaceous 1.
6.	Calyx lobes acute 0, acuminate 1, long-acuminate 2, rounded 3.
7.	Flowers radially symmetric 0, zygomorphic 1.
8.	Corolla aestivation overlapping 0, valvate 1.
9.	Flower shape narrow tube 1, salverform 2, open 0, campanulate 3.
10.	Corolla color green/white 0, purple-purplish green 1, red, orange, or yellow 2.
11.	Filaments straight 0, declinate 1.
12.	Filament tube absent 0, present 1.
13.	Filament base glabrous 0, pubescent 1.
14.	Filament base pubescence dense 0, sparse 1.
15.	Filaments inserted in anther basally 0, dorsally 1, ventrally 2.
16.	Anthers included in the corolla tube 1, at mouth of corolla tube 0, exserted 2.
17.	Anthers dehiscing separately 0, confluent 1.
18.	Ovary superior 0, partially inferior 1.
19.	Ovary \pm conical 0, narrowly beaked 1.
20.	Fruit pericarp membranous 0, coriaceous 1.
21.	Seeds reniform 0, rectangular 1.
22.	Cells in center of testa square 0, elongate 1.
23.	Lateral cell walls straight 0, sinuate 1.
24.	Dried seed color pale brown 0, dark brown 1, orange 2.
25.	Undigested seed surface pitted 0, smooth 1.
26.	Spiny supratectal processes absent 0, present 1.
27.	Colpi extending nearly to the poles 0, relatively short 1.
28.	Pollen without Ubisch bodies 0, covered with Ubisch bodies 1.
29.	Colpi with continuous margins 0, alongate apertures 1.
30.	Exine around apertures thickened 0, not thickened 1.
31.	Tectum continuous 0, not continuous 1.
32.	Beak-like margo apertures absent 0, present 1.
33.	Colpus border not thickened 0, thickened 1.
34.	Outline in equatorial view spherical 0, oblate 1.
35.	Outline in polar view obtuse, convex 0, acute, straight 1.
36.	Nexine same thickness as the sexine 0, nexine thicker than the sexine 1.

phies, both molecular (Olmstead & Sweere, 1994; Olmstead, pers. comm.) and morphological.

The data matrix is presented in Table 3. Most of the characters are self-explanatory; those peculiar to the Juanulloeae are described in detail here and the palynological characters were discussed in

Table 3. Data matrix used for the analysis of the Juanulloaeae.

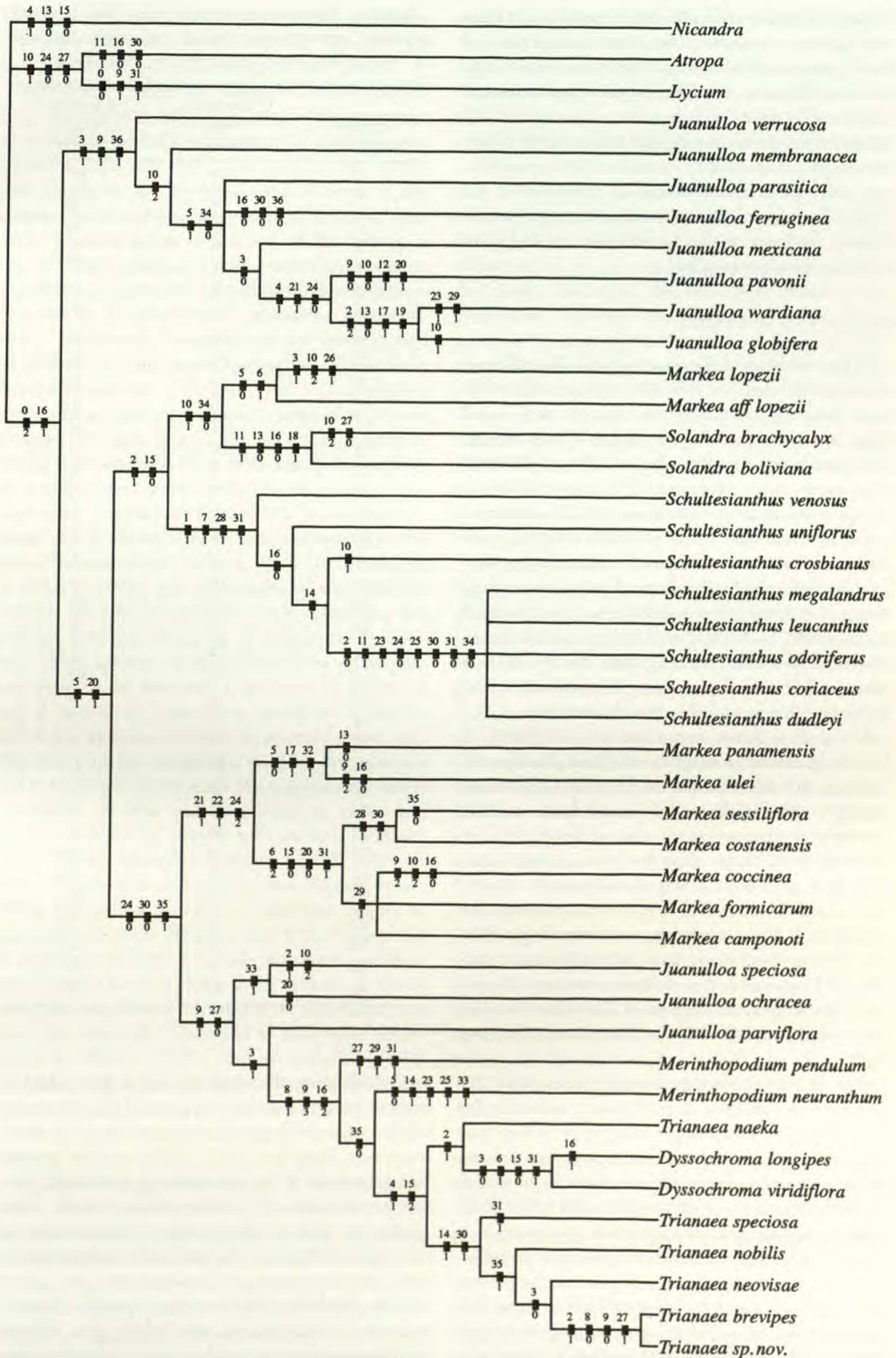
<i>Nicandra</i>	10001000000000?0200000001001001000100
<i>Atropa</i>	1000000000110101000000000000000000100
<i>Lycium cestroides</i>	0000000001100101200000000000001100100
<i>Solandra brachycalyx</i>	20100100002100?0001010001000001000000
<i>Solandra boliviana</i>	20100100001100?000101?????01001000000
<i>Markea sessiliflora</i>	2000012000000100100001102001101100100
<i>Markea costanensis</i>	200001200000010010000?????01101100110
<i>Markea coccinea</i>	2000012002200100000001102001010100110
<i>Markea formicarum</i>	2000012000000100100001102001010100110
<i>Markea camponoti</i>	2000012000000100100001102001010100110
<i>Markea lopezii</i>	20110010002001001000???????11001000000
<i>Markea aff. lopezii</i>	20100010001001001000?????????????????
<i>Markea panamensis</i>	20000000000000?1110011102001000010110
<i>Markea ulei</i>	2000000002000101010011102001000010110
<i>Merinthopodium neuranthum</i>	2001000013000111200010010100000001100
<i>Merinthopodium pendulum</i>	200101001300010?2000???????01010100110
<i>Schultesianthus uniflorus</i>	2110010100000100?0001?????01101100100
<i>Schultesianthus venosus</i>	211001010000010010001?????01101100100
<i>Schultesianthus crosbianus</i>	2110010100100110000010001001101100100
<i>Schultesianthus megalandrus</i>	2100010100010110000010010101100000000
<i>Schultesianthus leucanthus</i>	2100010100010110000010010101100000000
<i>Schultesianthus odoriferus</i>	210001010001011000001?????01100000000
<i>Schultesianthus coriaceus</i>	2100010100010110000010010101100000000
<i>Schultesianthus dudleyi</i>	210001010001011000001?????01100000000
<i>Juanulloa pavonii</i>	2000110000001101100011000001001000001
<i>Juanulloa wardiana</i>	20201100012000?1110101010001011000001
<i>Juanulloa globifera</i>	20201100011000?111010?????????????????
<i>Juanulloa speciosa</i>	2010010001200101100010000000000001110
<i>Juanulloa ochracea</i>	2000010001000101100000000000000001110
<i>Juanulloa parasitica</i>	2001010001200101100000001001001000001
<i>Juanulloa ferruginea</i>	2001010001200101000000001001000000000
<i>Juanulloa membranacea</i>	20010000012001011000???????01001000101
<i>Juanulloa verrucosa</i>	20010000010001011000?0001001001000101
<i>Juanulloa parviflora</i>	20010100010001011000???????????????????
<i>Juanulloa mexicana</i>	2000010001200101100000001001001000001
<i>Dyssochroma longipes</i>	20101110130001001000???????00000100100
<i>Dyssochroma viridiflora</i>	20101110130001002000???????00000100100
<i>Trianaea speciosa</i>	2001110013000112200010000000001100100
<i>Trianaea brevipes</i>	2010110000000112200010000001001000110
<i>Trianaea neovisae</i>	200011001300011220001?????????????????
<i>Trianaea nobilis</i>	2001110013000112200010000000001000110
<i>Trianaea naeka</i>	20111100130001022000???????00000000100
<i>Trianaea sp4</i>	201011000?000?????000?????????????????

Persson et al. (1994). Minute, peltate, glandular trichomes (character 1) on the leaves of *Schultesianthus* were first described by Bernardello and Hunziker (1991) and are either present or absent on both leaf surfaces. These trichomes are sunken into

small pits in the mesophyll so that the ca. 24 cell head is at about the same level as the foliar surface. The trichomes appear as minute reddish dots to the naked eye and are usually, but not always, more abundant on the abaxial leaf surface. Corolla aes-

→

Figure 4. One of the two equally parsimonious cladograms from the Hennig86 analysis. The tree shown here is identical to that produced by NONA, and to the consensus tree. The characters are discussed in the text, and character states are shown in Table 2. For characters marked on the branches of the cladogram: stippled marks indicate reversals and parallelisms (homoplasy) and solid marks non-homoplastic synapomorphies.



tivation (character 8) has been coded as either overlapping or valvate. The exact arrangement of overlapping corolla lobes in bud is sometimes difficult to determine from herbarium specimens and occasionally varies in a species or genus. Corolla ontogeny has not shed any light on the relative plesiomorphy or apomorphy of such differing aestivation patterns in the Acanthaceae (Scotland et al., 1994). Thus, should this character be used in subsequent analyses of the Juanulloeae, it should be unordered and unweighted.

RESULTS AND DISCUSSION

In the analysis of the genera of the Juanulloeae, two trees of length = 129, CI = 35, and RI = 71 were found by Hennig86 (see Fig. 4), and one of these two trees was also found by NONA. If only *Nicandra* is used as the outgroup, Hennig86 finds three trees, again of length 129, one of which is identical to the strict consensus tree. The two trees found by Hennig86 using all three outgroup taxa differ only in the resolution of *Schultesianthus*, with tree 2 being over-resolved owing to character state assignment from missing data. Tree 1 is identical to that found by NONA, which does not attempt to resolve nodes with missing data. In the NONA analysis, 15 of 50 replications were of length 129, indicating this is probably the shortest tree.

Using successive approximation weighting in Hennig86 character weights stabilized after four iterations, giving 444 trees of L = 280, CI = 67, and RI = 88. Reading all 444 trees back onto the unweighted data set gave trees of length 135 or 136, which is longer than the most parsimonious trees by 6 or 7 steps. Using the alternative weighting system of Goloboff (1993) we obtained one tree of length = 130 (not shown), one step longer than our most parsimonious tree generated using unweighted data. This tree differs in the positions of the three anomalous species of *Juanulloa* (see below) and in the order of branching in the *Trianaea* clade.

The stabilized weights from the successive approximation weighting analysis are presented in Table 4. Weights of 10 imply perfect fit to the tree, while weights of 0 (and lower numbers in the PeeWee analysis) imply the character is of poorer fit. Of the characters with weights of 10 in the Hennig86 analysis, two (character 12, presence of a filament tube, and character 26, presence on pollen of spiny suprategal processes) are uninformative (autapomorphic) and do not contribute to group formation on the tree. Only nine other characters had weights of 10, while the rest had low weights of 5

Table 4. Stabilized character weights from Hennig86 successive approximation analysis and weights (character fit) from PeeWee analysis (see text for explanation).

Character number	Character weight Hennig86	Character weight PeeWee
0	10	10
1	10	10
2	3	4.2
3	0	4.2
4	1	4.2
5	0	4.2
6	5	7.5
7	10	10
8	10	10
9	5	4.2
10	0	2.5
11	2	6
12	10	
13	1	5
14	2	5
15	2	4.2
16	1	3
17	3	7.5
18	10	10
19	10	10
20	1	5
21	4	7.5
22	10	10
23	1	6
24	2	5
25	3	7.5
26	10	
27	1	5
28	4	7.5
29	1	6
30	0	3.3
31	0	3.3
32	10	10
33	2	7.5
34	1	5
35	0	6
36	10	10

to 0, indicating the data set has a great deal of homoplasy and very low support. Of the characters traditionally used to define genera in the Juanulloeae (see Hunziker, 1977, 1979), corolla aestivation (character 8 in our analysis) and floral symmetry (character 7) perform better, while other characters, such as the insertion of the filament on the anther (character 15), are less consistent on our tree. Micromorphological characters such as the minute glandular trichomes characteristic of *Schultesianthus* (character 1, see below), the relative thicknesses of sexine and nexine layers in pollen

(character 36), and some pollen aperture characters (character 32) are a good fit to the tree and are useful in resolving relationships in this group.

Four main clades are identified in the Juanulloeae. The tribe is defined relative to the outgroups by its epiphytic habit (character 0), and the presence of anthers included in the mouth of the corolla tube (character 16, reversed several times in the group). The first clade, comprising species of *Juanulloa*, is sister group to the rest of the tribe (see Fig. 4). The members of this clade share synapomorphies in characters 3 (elongate inflorescence—reversed in *J. wardiana*, *J. globifera*, *J. pavonii*, and *J. mexicana*), 9 (narrow tubular flowers), and 36 (pollen with the nexine thicker than the sexine). *Juanulloa pavonii* + (*J. wardiana* + *J. globifera*) share a large suite of characters, many of which are shared with other taxa in the tribe (i.e., homoplasious): these include calyx lobes equal in length to the corolla tube (character 4) and pale brown, reniform seeds (characters 21 and 24). *Juanulloa wardiana* and *J. globifera* have been segregated as the genus *Rahowardiana* (D'Arcy, 1973 [1974]; Knapp & D'Arcy, 1993), but the results of this analysis indicate their relationships lie with *Juanulloa*, and perhaps they are deserving of subgeneric recognition. Three species of *Juanulloa* are in an anomalous position on the tree: *J. speciosa*, *J. ochracea*, and *J. parviflora*. *Juanulloa parviflora* is known only from the type, which bears a single flower, and thus many of the characters used in this analysis had to be scored as missing. Missing data can affect placement of taxa and resolution of trees and should therefore be viewed with caution (Platnick et al., 1991). *Juanulloa speciosa* and *J. ochracea* share a distinctive pollen type (see Persson et al., 1994) and pollen characters contribute largely to their position in the *Trianaea* (see below) clade. We do not have confidence in this placement, and thus have elected to keep these three species in *Juanulloa* pending further investigation. *Juanulloa speciosa* was originally described as the genus *Sarcophysa* by Miers (1857), and is morphologically somewhat isolated in the genus. The relationship of these taxa to the rest of *Juanulloa* is a subject that would bear investigation using molecular techniques.

The second main clade consists of *Markea lopezii* and a related, undescribed taxon, the species of *Solandra* treated in this analysis and the genus *Schultesianthus*. This clade is united by the possession of solitary flowers (character 2, reversed in part of *Schultesianthus*) and basifixed anthers (character 15, in parallel with several other taxa in the tribe). *Markea lopezii* and its undescribed relative

are both known only from flowering specimens, and thus the matrix has many missing entries. *Markea lopezii* has anomalous pollen in the group, with prominent spiny supracteal processes (Persson et al., 1994), and its relationships need to be investigated further. Not all species of *Solandra* were included in this analysis, but these results indicate that it along with *M. lopezii* and *M. aff. lopezii* are the sister group to *Schultesianthus* and thus should be included in the tribe. However, cpDNA results (Olmstead et al., in press), using only four taxa of the group (*Solandra*, *Markea*, *Dyssochroma*, and *Juanulloa*), indicate that *Solandra* is the sister group of the rest of the Juanulloeae. Since no species of *Schultesianthus* were sampled in the cpDNA studies, this potential conflict remains to be solved. Many of the species of *Schultesianthus* were first described as *Solandra* (see Conspectus) owing to their close morphological similarity, and the species now recognized as *Schultesianthus* were thought to be intermediate between *Markea* and *Solandra* by D'Arcy (1973 [1974]).

All the species of *Schultesianthus* share a number of synapomorphies, two of which (character 1, peltate glandular trichomes and character 7, zygomorphic flowers) are found nowhere else on the tree. The genus also has two pollen synapomorphies: character 28, copious Ubisch bodies, and character 31, a discontinuous tectum (Persson et al., 1994). *Schultesianthus venosus*, *S. uniflorus*, and *S. crosbianus* differ from the rest of the genus as traditionally defined (see Bernardello & Hunziker, 1991) in their flowers with non-declinate stamens and style, but share all other synapomorphies of the group (see also Conspectus and D'Arcy, 1973 [1974]). These species are known from very few collections.

The genus *Markea* comprises the third main clade, united by the possession of pale tan (character 24) and rectangular seeds (character 21) with elongate testal cells (character 22) (see Fig. 4). The species *M. panamensis* and *M. ulei* have been separated as the genus *Hawkesiophyton* (Hunziker, 1977) and are probably worthy of subgeneric status. A species not treated in this analysis (it is known only from the type, which consists of a single poorly preserved flower), *M. sturmii* Cuatr., is superficially similar to *M. ulei* and should be examined more closely. The peculiar seed type seen in *Markea* is perhaps related to ant dispersal, as most of the species in this group are associated with ants in various ways (see above and Ducke, 1915). Many ant-dispersed seeds bear large elaiosomes (oil or fat bodies) that make them attractive to ants (see references in Willson, 1983). This is apparently not



Figure 5. SEM of seeds of *Markea coccinea* Rich. (Brazil, *Krukoff 6531*, BM).—A. Whole seed, scale bar = 278 μm .—B. Close-up of tectal surface, scale bar = 34.5 μm .

the case in *Markea* (see Fig. 5), but fresh material must be examined to determine this for certain. In the genus *Datura*, the elaiosome often drops off when plants are dried and mounted on herbarium sheets (see Persson et al., in press). The seeds of *Markea* seem to have a fine reticulum of sticky threads on top of the testa (see Fig. 5B), which may make them stick to ants, thus causing them to be deposited in ant gardens.

The fourth clade in the tribe is that containing the genera *Merinthopodium*, *Dyssochroma*, and *Trianaea*. Three species of *Juanulloa* are also present in this clade, but as discussed above, are probably not correctly placed here. The clade (minus the species of *Juanulloa*) is united by synapomorphies in characters 8 (valvate aestivation, reversed in some species of *Trianaea*), 9 (campanulate flowers), and 16 (filaments exerted from the corolla tube). In general members of this clade all possess large, campanulate, greenish or greenish purple flowers

(see Fig. 3) that are pollinated by bats (Vogel, 1958; Cuatrecasas, 1959; Baker, 1973; Voss et al., 1980). Voss et al. (1980), studying *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. at Finca La Selva, Costa Rica, postulated that it was adapted for pollination by trampling bats, as the flowers fell early in the night, were borne singly, and were odorless. Like many of the other species of the Juanulloae these plants are only rarely collected, but in addition to this, each sheet often consists only of a single flower, making dissection undesirable and incompatible with the preservation of the specimen (this has also been noted as a problem in the study of *Solandra*; see Bernardello & Hunziker, 1987). The distinctive filament base morphology mentioned in the generic description is not visible in pressed specimens, but is likely to occur in all species of *Trianaea*. Ovary structure, a character that would separate *Trianaea* (with a 4–5-carpellate, 8–10-loculate ovary) from *Merinthopodium* and *Dyssochroma* (with bicarpellate, 4-loculate ovaries), can only rarely be assessed even with fruiting specimens.

We showed (Persson et al., 1994) that the twelve pollen types in the tribe did not cut across the boundaries of the main clades. However, although they serve effectively for the purposes of identification, palynological characters alone provided little resolution of relationships among the taxa. The inclusion of palynological characters in the present analysis increases the number of character states that can be sampled from the relatively few specimens that are available for many of the species. It contributes to the resolution of relationships and may also serve to identify functionally correlated syndromes of characters, such as those found in bat-pollinated species.

This analysis clearly highlights some of the problems with the characters used to identify and recognize the genera of the Juanulloae. As previously defined, the genera were not monophyletic although many of the characters used in their definition are phylogenetically informative. The relationships of the monophyletic groups we have recognized in this study have not been fully resolved. The weak support for the basal clades in our tree indicates that more work is needed at this level within the tribe. Many of the genera have never been adequately monographed, and field-based studies will prove essential for the ultimate resolution of phylogenetic relationships in the group as additional characters that may prove useful are likely to be found in living plants. The extension of molecular systematics to a more comprehensive sample of the species may

also help to resolve many of the remaining uncertainties.

CONSPECTUS OF THE JUANULLOEAE
(INCLUDING *SOLANDRA*)

This generic conspectus is designed to allow the reader to identify herbarium specimens and, to some extent, living plants. For each genus a description, a list of the species, and references to published monographs or illustrations are provided. The species not included in the cladistic analysis are indicated with asterisks. Synonyms are listed after each accepted name. Directions for further investigation and work in progress are discussed for each genus.

- 1a. Corolla limb broadly campanulate, greenish or yellow, more than 5 cm long.
 - 2a. Corolla yellow sometimes with purplish streaks in the throat (bluish in *S. boliviana*), usually greater than 13 cm long, the stamens declinate; ovary somewhat inferior 6. *Solandra*
 - 2b. Corolla greenish or greenish purple, usually less than 13 cm long, the stamens regular; ovary completely superior.
 - 3a. Corolla veneration imbricate (occasionally valvate); anthers ventrifixed; filaments conspicuously geniculate at the base, covering the nectary; ovary 8–10-locular 7. *Trianaea*
 - 3b. Corolla veneration valvate; anthers either basifixed or dorsifixed; filaments not conspicuously geniculate; ovary bilocular.
 - 4a. Anthers basifixed; inflorescences consisting of a single flower; SE Brazil in Atlantic forest 1. *Dysochroma*
 - 4b. Anthers dorsifixed; inflorescences of 1–many flowers, with long and flexible axes; Central and N South America 4. *Merinthopodium*
- 1b. Corolla limb tubular to narrowly campanulate, not broadly campanulate and bell-shaped, variously colored, cream to bright orange, usually less than 5 cm long.
 - 5a. Flowers zygomorphic, at least somewhat (difficult to see in pressed specimens of some species), cream fading yellowish, sweetly fragrant; calyx thick and coriaceous, drying somewhat woody; leaves with minute peltate glandular trichomes on both surfaces; stems pubescent in new growth 5. *Schultesianthus*
 - 5b. Flowers regular, orange, cream or greenish, not fragrant; calyx various, but not drying woody; leaves lacking minute peltate glandular trichomes; stems glabrous or pubescent.
 - 6a. Anthers basifixed; corolla funnelliform or infundibuliform, usually yellowish or greenish (bright orange-red and nearly salverform in *M. coccinea*), the tube and lobes membranous in texture; fruit thin-



Figure 6. *Dysochroma viridiflora* (Sims) Miers (Sims, J. 1818. Curtis's Botanical Magazine 45: t. 1948).

- walled, the seeds elongate, pale or orange 3. *Markea*
- 6b. Anthers dorsifixed; corolla narrowly tubular (in *J. pavonii* the tube very short), white, orange or reddish, the tube and lobes thick and fleshy in texture; fruit not thin-walled as above, often somewhat woody, the seeds reniform, usually dark brown 2. *Juanulloa*

1. *Dysochroma* Miers, Ann. Mag. Nat. Hist. ser. 2, 4: 250. 1849. TYPE: *Dysochroma viridiflora* (Sims) Miers (basionym: *Solandra viridiflora* Sims, 1818). Figure 6.

Epiphytic shrubs or small trees, occasionally terrestrial; stems pendulous, the bark thin, flexible and exfoliating, drying a dark, reddish brown. Leaves elliptic, 5–12 × 2.5–5 cm, coriaceous, glabrous. Inflorescence terminal, a highly modified cyme, congested, often consisting of a single flower,

glabrous. Buds elliptic, the corolla aestivation valvate. Pedicels glabrous. Flowers with the calyx divided nearly to the base, the lobes 3–4 cm long, triangular, acuminate at the tips, coriaceous, glabrous; corolla greenish or greenish purple, broadly flaring to campanulate, the tube 5–6 cm long, the lobes 1–2.5 cm long, at anthesis strongly reflexed; filaments adnate to the corolla tube in the lower $\frac{1}{3}$, exserted or included, 7–9 cm long, glabrous along their whole length; anthers basifixed, 1–1.5 cm long; pollen 3-colporate with long colpi and uneven reticulate ornamentation; ovary superior, glabrous; style glabrous, 8–10 cm long, the stigma clavate. Fruit and seeds not known. 2 spp., SE Brazilian rainforests.

List of species. *Dysochroma longipes* (Sendtn.) Miers, Brazil (*Markea longipes* (Sendtn.) Cuatr., *Solandra longipes* Sendtn.); *D. viridiflora* (Sims) Miers, Brazil (*Dysochroma albidoflavum* Lemaire, *Markea peckoliorum* Gilg, *M. viridiflora* (Sims) Ducke, *Solandra viridiflora* Sims).

Dysochroma may be congeneric with *Trianaea*, but since so few specimens of these plants are known and nothing is known about the fruits or seeds, we have maintained it as distinct pending further investigation. The pollen is identical to most species of *Trianaea* but differs from that of *T. speciosa* in that the reticulate ornamentation is discontinuous, so that areas close to the poles lack muri (see Persson et al., 1994).

The two described species of *Dysochroma* are in fact only different stages of floral development (L. F. de Carvalho, pers. comm.), with the included anthers of *D. longipes* occurring at earlier stages of flowering, while the exserted anthers of *D. viridiflora* are often seen on flowers found on the forest floor post-flowering. Future studies being carried out at the Jardim Botânico de Rio de Janeiro will clarify this situation.

2. Juanulloa Ruiz & Pavón, Prodr. Fl. Peruv. 27, t. 4. 1794. TYPE: *Juanulloa parasitica* Ruiz & Pavón. Figures 2A, 7.

- Ectozoma* Miers, Ann. Mag. Nat. Hist. ser. 2, 3: 166. 1849. TYPE: *Ectozoma pavonii* Miers.
Laureria Schlechtendahl, Linnaea 8: 513. 1833. TYPE: *Laureria mexicana* Schldl.
Portaea Tenore, Atti 7a. Adum. Sc. Ital. 902, t. 1846. TYPE: *Portaea aurantiaca* Tenore.
Rahowardiana D'Arcy, Ann. Missouri Bot. Gard. 60: 670. 1973 [publ. 1974]. TYPE: *Rahowardiana wardiana* D'Arcy.
Sarcophysa Miers, Ann. Mag. Hist. ser. 2, 4: 190. 1849. TYPE: *Sarcophysa speciosa* Miers.
Ulloa Pers., Syn. Pl. 1: 128. 1805. TYPE: *Juanulloa parasitica* Ruiz & Pavón.

Epiphytic shrubs or small trees, the stems often hanging and pendulous from the canopy, 1–20 m; bark of stems loose and exfoliating when dry, often reddish or reddish brown. Leaves elliptic, ovate or obovate, 6–30 × 5–9 cm, usually petiolate (sessile in *J. verrucosa*), membranous or coriaceous, glabrous or pubescent, the trichomes uniseriate, simple or more often branched. Inflorescence terminal or lateral, a variously modified cyme, occasionally somewhat raceme-like, often many times branched, the peduncle often very long and pendulous, usually many flowered (10–50) but occasionally reduced to 1–2 flowers (*J. speciosa*), glabrous or pubescent, the trichomes uniseriate, simple or branched, buds elongate, usually exserted from the calyx tube, corolla aestivation quincuncial or imbricate. Flowers with the calyx lobed nearly to the base or unlobed and inflated (*J. speciosa*), usually somewhat fleshy and bright colored, $\frac{1}{3}$ to equal to the length of the corolla tube; corolla fleshy, funnelform to narrowly tubular, 1–9 cm long, red, orange, or cream with reddish or purple markings, the tube either flaring at the apex (*J. pavonii*, *J. ferruginea*) or more commonly slightly constricted, the lobes minute and rounded or equal in length to the tube (*J. pavonii*, *J. ferruginea*); filaments inserted near the base or ca. $\frac{1}{2}$ way along the tube, densely pubescent with uniseriate trichomes at the point of insertion; anthers included in the corolla tube at anthesis, very variable in size, dorsifixed; pollen 3-colporate, either with long, narrow colpi and scabrate-rugulate ornamentation or with short, broad colpi and a scabrate-perforate ornamentation; ovary ovoid to conical or beaked (*J. wardiana*, *J. globifera*), glabrous; style glabrous, \pm equal to the filaments, usually somewhat longer at anthesis, the stigma capitate to somewhat clavate, bilobed. Fruit green berry, ovoid to conical, usually within the accrescent calyx, 1–3 cm long (in *J. wardiana* and *J. globifera* seeds are borne in the ovary beak, but mature fruits are unknown); seeds reniform, quite large, 2–7 × 1.5–3 mm, dark brown or reddish brown. 11 spp., Mexico to Bolivia.

Literature. Hunziker & Subils (1991).

List of species. *Juanulloa ferruginea* Cuatr., Colombia to Peru; *J. globifera* (S. Knapp & D'Arcy) S. Knapp, NW Colombia (*Rahowardiana globifera* S. Knapp & D'Arcy); *J. membranacea* Rusby, Bolivia (*J. pedunculata* Rusby); *J. mexicana* (Schlechtendahl) Miers, Mexico and Central America to N Colombia (*J. aurantiaca* Otto & Dietr., *J. bicolor* Gleason, *J. elliptica* Dunal, *J. hookeriana* Miers, *J. panamensis* Miers, *J. sargii* Donn. Sm., *Laureria mexicana* Schlechtendahl, *Markea tomentosa* Lun-

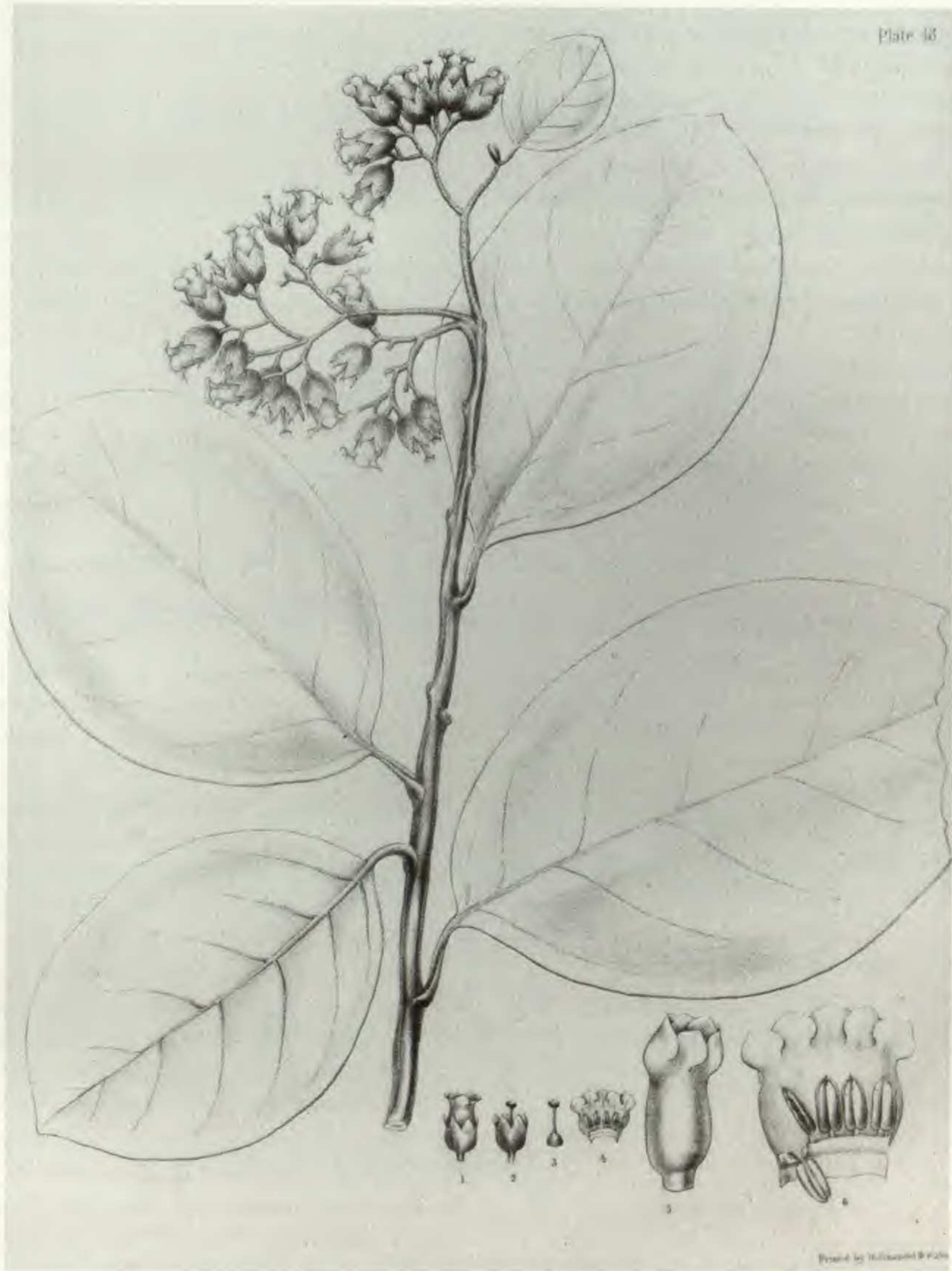


Figure 7. *Juanulloa pavonii* (Miers) Benth. & Hook. as *Ectozoma Pavonni* (plate 48 from Miers, J. 1857. Illustrations of South American Plants).

dell, *Portaea aurantiaca* Tenore); *J. ochracea* Cuatr., Colombia to Peru; *J. parasitica* Ruiz & Pavón, Ecuador, Peru, and Brazil (*Ulloa parasitica* (Ruiz & Pavón) Pers.); *J. parviflora* (Ducke) Cuatr., Brazil, near Manaus (known only from the type) (*Markea parviflora* Ducke); *J. pavonii* (Miers) Benth. & Hook., W Ecuador and NW Peru (*Ectozoma pavonii* Miers, *Markea pavonii* (Miers) D'Arcy); *J. speciosa* (Miers) Dunal, Colombia and Ecuador (*Sarcophysa speciosa* Miers); *J. verrucosa* (Rusby) Hunz., Bolivia (*Markea verrucosa* Rusby);

J. wardiana (D'Arcy) S. Knapp, Panama (*Rahowardiana wardiana* D'Arcy).

The flowers of most of the species of *Juanulloa* conform to the classic hummingbird pollination syndrome: they are tubular, brightly colored and very thick and fleshy (Fig. 2A). However, *J. pavonii* (Fig. 7) and *J. ferruginea* (and also perhaps to some extent *J. parviflora*) have quite different flowers, which are greenish, with shorter tubes and somewhat reflexed lobes. These perhaps represent a different pollination syndrome.

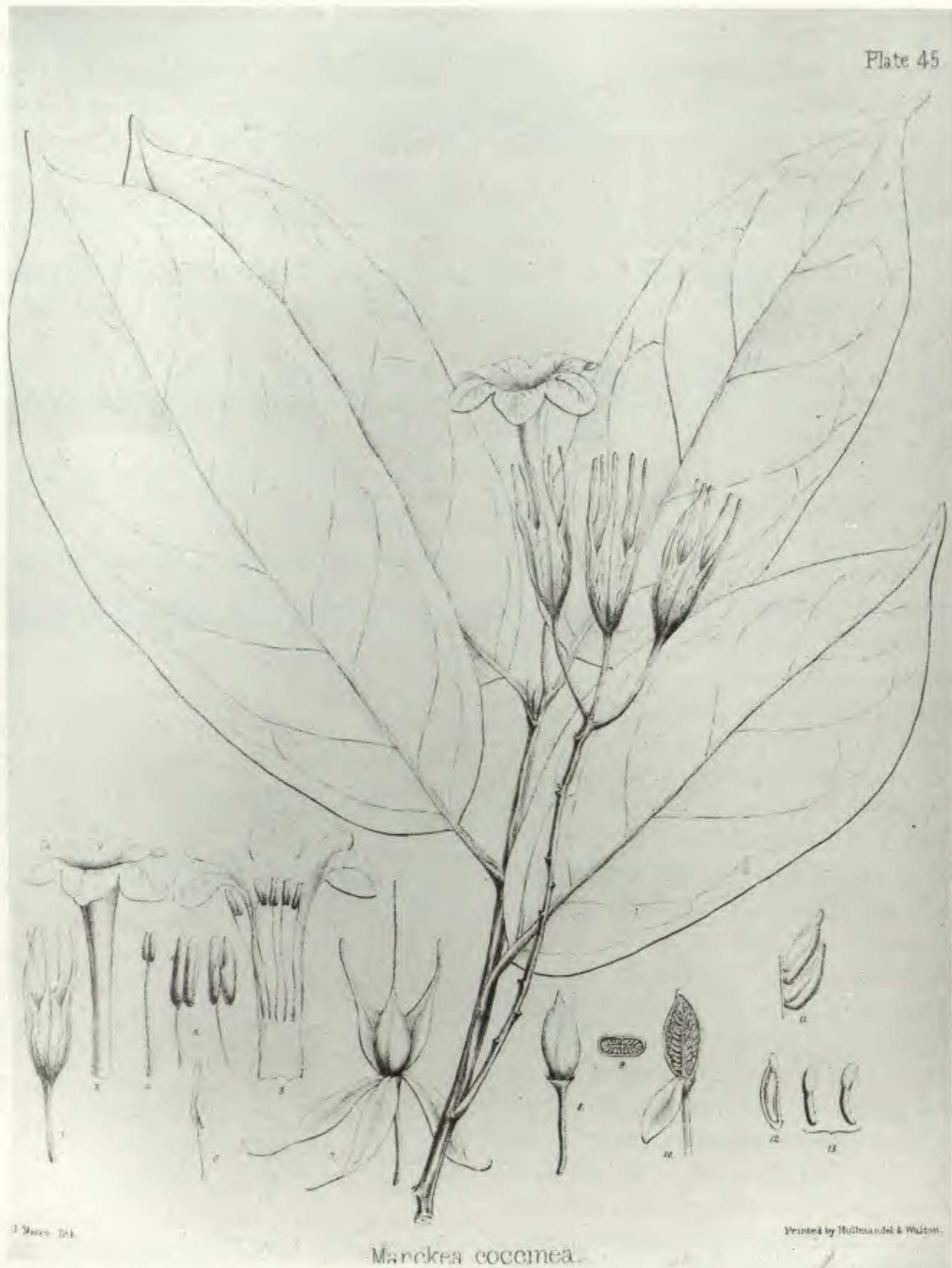


Figure 8. *Markea coccinea* Rich. (plate 45 from Miers, J. 1857. Illustrations of South American Plants).

The very condensed globular inflorescence of *Juanulloa wardiana* and *J. globifera* is unique in the tribe, and in the family Solanaceae (illustrations can be seen in Knapp & D'Arcy, 1993). In these species the calyx as well as the corolla is brightly colored and quite showy. These flowers are apparently visited by hummingbirds, and produce copious nectar.

There are two types of pollen found in this genus (Persson et al., 1994). In *Juanulloa speciosa* and *J. ochracea* the pollen is 3-colporate with long, narrow colpi and scabrate/rugulate exine ornamentation. In

the rest of the genus the pollen is 3-colporate with short, broad colpi and a scabrate/perforate exine ornamentation.

3. *Markea* Rich., Actes Soc. Nat. Hist. Paris 1: 107. 1792. TYPE: *Markea coccinea* Rich. Figure 8.

Hawkesiophyton Hunz., Kurtziana 10: 39. 1979. TYPE: *Hawkesiophyton panamense* (Standl.) Hunz. (basionym *Markea panamensis* Standl.).

Lamarkea Pers., Synopsis 1: 218. 1805. TYPE: *Lamarkea*

coccinea (Rich.) Pers. (basionym *Markea coccinea* Rich.).

Epiphytic shrubs or small trees, occasionally growing on the forest floor in cloud forest. Leaves elliptic to ovate, 5–25(–40) × 2.5–10(–20) cm, coriaceous or membranous, glabrous or pubescent, the trichomes simple and uniseriate, multicellular. Inflorescence a variously modified cyme, sometimes superficially raceme-like, branched or simple, glabrous to minutely pubescent, ± sessile (*M. sessiliflora*), to borne on an elongate peduncle (*M. coccinea*), 1–25 cm long, bearing 1–10 flowers at a time, but with many scars, data on specimen labels indicating that only one flower opens at a time. Buds elongate, corolla aestivation imbricate or cochlear. Pedicels glabrous or pubescent. Flowers with the calyx lobed nearly to the base, the lobes long-triangular, 0.8–3 cm long, often with distinctively colored venation and long-acuminate tips, glabrous or pubescent; corolla bright orange (*M. coccinea*) or more often greenish purple or cream colored, salverform (*M. coccinea*) to funnellform, the tube 1–7 cm long, the lobes 0.5–1.2 cm long, rounded and the margins occasionally somewhat lacinate, not reflexed at anthesis, glabrous or pubescent with simple, uniseriate trichomes on the exterior surfaces; filaments adnate to and included in the corolla tube, ± equal in length to the corolla tube or ca. ½ its length, pubescent at the point of insertion; anthers basifixed, elongate, ca. 2 mm (*M. ulei*, *M. panamensis*) to ca. 1 cm (*M. sessiliflora*, *M. camponoti*) long, longitudinally dehiscent; pollen 3-colporate, ornamentation and apertures varying; ovary superior, glabrous; style usually equal in length with the filaments, or longer and held at the mouth of the corolla tube, the stigma clavate. Fruit an ellipsoid berry, 1–2 × ca. 1 cm, green when ripe, the apex somewhat beaked from the persistent style base, the pericarp thin and papery when dry, in herbarium specimens often almost translucent, held within the accrescent calyx; seeds many, long rectangular, 2–5 × ca. 0.5 mm, usually bright orange. 9 spp., Panama to S Peru.

List of species. *Markea camponoti* Ducke, upper Amazon basin; *M. coccinea* Rich., upper Amazon basin to the Guianas (*Lamarckea coccinea* Pers.); *M. costanensis* Steyerl., Venezuela, Cordillera de la Costa; *M. formicarum* Dammer, Amazon basin, on white sand; *M. longiflora* Miers, Trinidad (this may in fact be an older name for the taxon herein referred to as *M. camponoti*, but the species has not been recollected in Trinidad since the type specimen, which has a single, badly damaged flower); *M. panamensis* Standl., Panama and adjacent Co-

lombia (*Hawkesiophyton panamense* (Standl.) Hunz., *M. dimorpha* C. V. Morton); *M. sessiliflora* Ducke, N Amazon basin, Guianas, Roraima plateau (*M. porphyrobaphes* Sandwith, *M. reticulata* Steyerl. & Macguire); **M. sturmii* Cuatr., Colombia; *M. ulei* (Dammer) Cuatr., upper Amazon basin (*Ec-tozoma ulei* Dammer, *Hawkesiophyton klugii* Hunz., *H. ulei* (Dammer) Hunz.).

Markea as here defined is composed of two main clades, one consisting of the small greenish-flowered taxa previously treated as the genus *Hawkesiophyton*, *M. ulei* and *M. panamense*, which perhaps deserve sectional or subgeneric rank. *Markea sturmii*, not treated in the cladistic analysis, is somewhat intermediate between the small-flowered clade and the following. The other clade consists of five taxa, again divided into two clear groups: one with short inflorescences and flowers drying dark on the herbarium sheet (*M. sessiliflora*, *M. costanensis*) and the other consisting of mainly Amazonian species with long-acuminate calyx lobes with distinctive venation and usually elongate inflorescences.

The three types of pollen found in this genus (Persson et al., 1994) correlate closely with these groups. All are 3-colporate but they differ in exine sculpturing and aperture type. In *M. ulei* and *M. panamensis* the colpi are long and narrow and the apertures distinctly beaked. Short colpi occur in the *M. camponoti* type, where the ornamentation is baculate and in the *M. sessiliflora* type, where it is microreticulate to scabrate.

The genus *Markea* is in dire need of a field-based monograph.

4. *Merinthopodium* Donn. Sm., Bot. Gaz. 23: 11. 1897. TYPE: *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. (basionym: *Markea neurantha* Hemsl.). Figures 3A, 9.

Epiphytic shrubs or small trees, 1–10 m, often clambering over branches and hanging from the canopy; bark loose and exfoliating, bright silvery-gray. Leaves elliptic to obovate, occasionally strongly three-veined from the base, 10–15 × 5–9 cm, glabrous to minutely puberulent along the main veins beneath, the trichomes simple and uniseriate. Inflorescence an elongate, pendulous raceme, the peduncle 15–50 cm long, minutely pubescent with tuberculate trichomes with multiseriate bases bearing one or two uniseriate simple branches, the branches breaking off leaving the tuberculate bases which cause a warty roughened texture on the peduncle, flowers borne only at the tip or distal ¼, usually only 2–7 at a

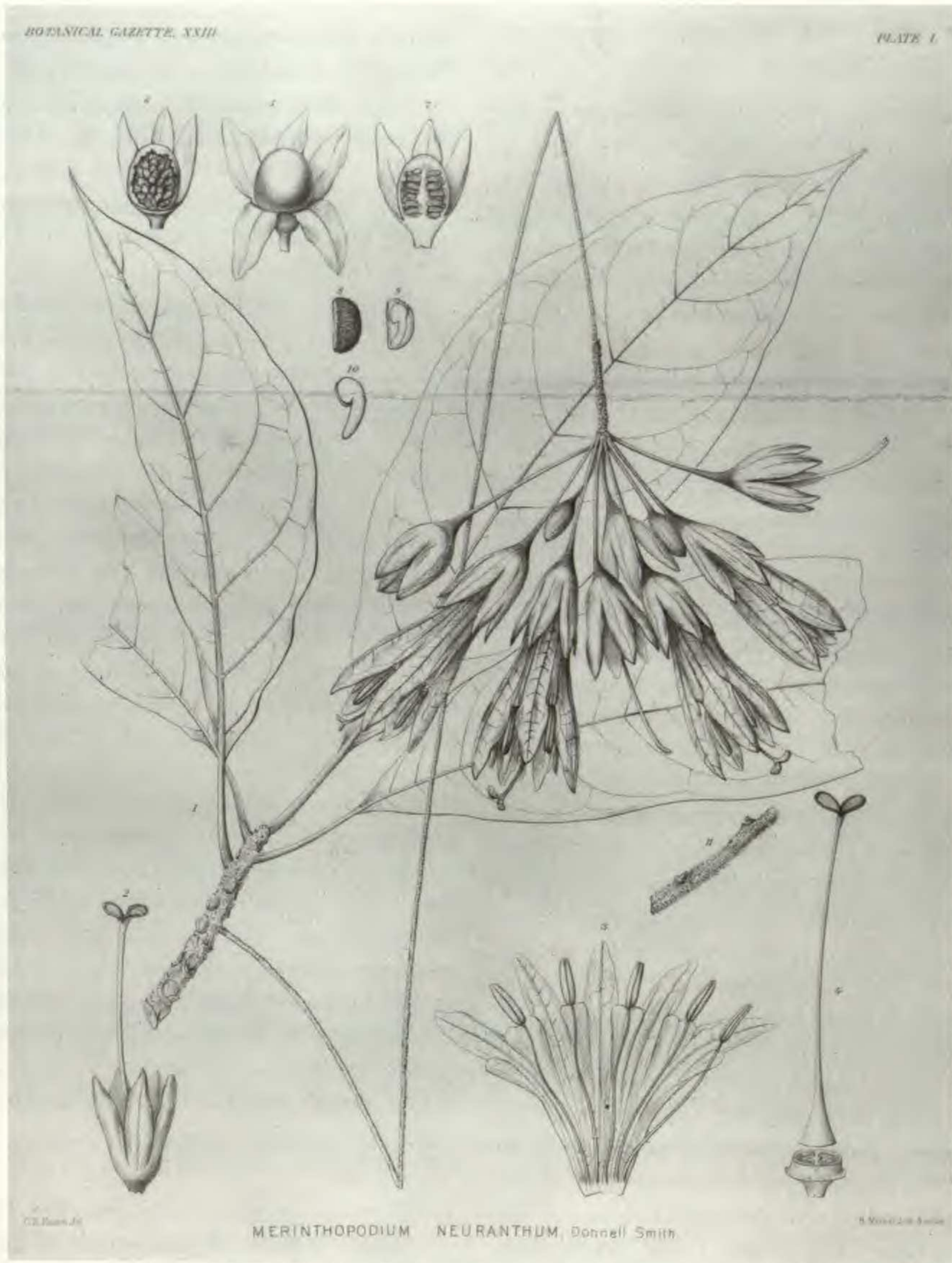


Figure 9. *Merinthopodium neuranthum* (Hemsl.) Donn. Sm. (plate from Donnell Smith, J. 1897. Bot. Gaz. (Crawfordsville) 23).

time, but the inflorescence with up to 100 scars. Buds ellipsoid, rapidly elongating to exceed the calyx tube, corolla aestivation valvate. Flowers with the calyx usually $\frac{1}{4}$ the length of the corolla tube at anthesis, membranous to coriaceous, lobed nearly to the base, the lobes with blunt tips; corolla greenish to greenish with various purple markings, the tube 3–10 cm long, flaring early in anthesis but at full anthesis broadly campanulate, the lobes ca. 2 cm long, strongly reflexed at anthesis; filaments adnate to the base of the corolla tube, exerted from it at anthesis, glabrous; an-

thers bright yellow, dorsifixed and somewhat versatile; pollen generally large, 3-colporate with scarate ornamentation and protruding apertures; ovary bilocular, glabrous; style glabrous, \pm equal to the length of the filaments at anthesis, the stigma capitate, bright green, strongly bi-lobed. Fruit a green berry, ovoid, 1–2.5 cm long, the pericarp \pm membranous, not leathery or woody; seeds many, 1.5–2 \times 0.5–1 mm, reniform, reddish brown. 3 spp., S Mexico to N Venezuela and Colombia.

List of species. *Merinthopodium neuranthum*

(Hemsl.) Donn. Sm., S Mexico and Central America (*Markea campanulata* (Donn. Smith) Lundell, *Markea gentlei* Lundell, *Markea internexa* (Blake) Lundell, *Markea leptesthema* (Blake) Cuatr., *Markea neurantha* Hemsl., *Me. campanulatum* Donn. Smith, *Me. internexum* Blake, *Me. leptesthemum* Blake); *Me. pendulum* (Cuatr.) Hunz., Colombia and Venezuela (*Markea pendula* Cuatr.); **Me. vogelii* (Cuatr.) Castillo & R. E. Schultes, Colombia and Venezuela (*Markea vogelii* Cuatr.).

The shape of the flowers of *Merinthopodium* depends greatly on their state when collected. These plants bloom at night and are probably pollinated by bats (see Voss et al., 1980). Thus flowers collected before full anthesis are shaped like a flaring tube, but when fully in bloom, the limb becomes broadly campanulate with strongly reflexed lobes. This same situation occurs in *Trianaea* and *Dyssochroa*. The peculiar trichomes found on the peduncle of *Merinthopodium* are also found in *T. naeka* S. Knapp of eastern Ecuador. One of the reasons why there are many synonyms in this genus is that specimens collected at different stages of flowering have been regarded as distinct species. There is also geographical variation in flower size and leaf texture.

5. *Schultesianthus* Hunz., Kurtziana 10: 35. 1977. TYPE: *Schultesianthus leucanthus* (Donn. Sm.) Hunz. (basonym: *Markea leucantha* Donn. Sm.). Figure 10.

Epiphytic shrubs or small trees, occasionally terrestrial in wet cloud forests; bark usually somewhat reddish, glabrous or pubescent with simple uniseriate trichomes on the new growth; leaves borne in congested groups separated by long naked internodes. Leaves elliptic, 6–15 × 2.5–9 cm, thick and coriaceous, drying pale green or brownish, often rounded at the tip, glabrous or pubescent with simple uniseriate trichomes, in addition all species bearing minute glandular trichomes each with a unicellular base and multicellular head sunk in a pit on the upper and lower surfaces, giving the appearance of small red dots on dry specimens. Inflorescence a terminal cyme, variously branched, occasionally reduced to a single flower (*Sch. crosbianus*), glabrous or variously pubescent with simple uniseriate trichomes. Buds elongate, the apex swollen, corolla aestivation quincuncial or cochlear. Pedicels glabrous or pubescent, usually quite short. Flowers with the calyx very coriaceous, lobed ½ way or nearly to the base, the lobes strongly overlapping, glabrous or minutely glandular pubescent, becoming woody and accrescent in fruit; corolla

funneliform to strongly infundibuliform, 4–15 cm long, occasionally somewhat zygomorphic, strongly and sweetly fragrant, pale green to cream (black in *S. crosbianus*), yellowing with age, the lobes rounded and often somewhat lacinate; filaments adnate with the corolla tube in the lower ⅓, densely pubescent at point of insertion and ca. ½ way to the anthers above, regular or declinate, exerted from the corolla tube at anthesis; anthers small and elliptic, or slightly larger and more elongate (in *Sch. venosus*, *Sch. uniflorus*, and *Sch. crosbianus* with non-declinate filaments); pollen 3-colporate, rugulate and covered in Ubisch bodies; ovary glabrous, somewhat pointed, bilocular; style declinate or straight, glabrous, the stigma broadly capitate, distinctly 2-lobed. Fruit a green to purplish green berry, 1–3 cm long, ovoid or somewhat pointed, woody when dry, very leathery and fleshy when fresh, invested in the accrescent woody calyx; seeds many, reniform, large, 5–6 × 3–4 mm, pale yellowish tan or dark brown. 8 spp., Mexico to Bolivia.

Literature. Bernardello & Hunziker (1991).

List of species. *Schultesianthus coriaceus* (Kuntze) Hunz., Antioquia, Colombia (*Solandra coriacea* Kuntze); *Sch. crosbianus* (D'Arcy) S. Knapp, Costa Rica and Panama (*Markea crosbiana* D'Arcy); *Sch. dudleyi* Bernardello & Hunz., S Ecuador, S Peru; *Sch. leucanthus* (Donn. Sm.) Hunz., S Mexico to S Peru (*Markea leucantha* Donn. Sm., *Merinthopodium leucanthum* (Donn. Sm.) Blake, *Metternichia werklei* Schumann ex Bois); *Sch. megalandrus* (Dunal) Hunz., N Colombia and N Venezuela (*Markea megalandra* (Dunal) D'Arcy, *M. suaveolens* Standl., *Metternichia ? megalandra* Dunal, *Sch. suaveolens* (Standl.) Hunz., *Solandra megalandra* (Dunal) Killip & Pittier); *Sch. odoriferus* (Cuatr.) Hunz., Cordillera Oriental, Colombia (*Solandra odorifera* Cuatr.); *Sch. uniflorus* (Lundell) S. Knapp, Chiapas, Mexico (*Markea uniflora* Lundell, *Merinthopodium uniflorum* (Lundell) Hunz.); *Sch. venosus* (Standl. & C. V. Morton) S. Knapp, Costa Rica and Panama (*Markea venosa* Standl. & C. V. Morton).

D'Arcy (1973 [1974]), in his treatment of *Markea* for Flora of Panama, clearly and correctly identified the close relationships between the species of the present genus *Schultesianthus*. He recognized the three radially symmetrical flowered species, *Sch. crosbianus*, *Sch. uniflorus*, and *Sch. venosus*, as members of the "perhaps generically distinct" group including *Sch. leucanthus* (as *Markea megalandra* in his treatment).

Many of the species of *Schultesianthus* were originally described as *Solandra*, and *S. boliviana* and *Sch. coriaceus* have been considered "linking" spe-



Figure 10. *Schultesianthus leucanthus* (Donn. Sm.) Hunz. (Hampshire & Whitefoord 469, BM).

cies. For discussion see comments with the generic description of *Solandra*.

The flowers of *Schultesianthus* are among the most showy in the Juanulloaeae (see Fig. 10). They are sweetly fragrant and change color from white to a creamy yellow with age. Large bees have been observed visiting the flowers, but little is known about their biology.

6. *Solandra* Swartz, nom. cons., Kongl. Vetensk. Acad. Nya Handl. 8: 300–306. 1787. TYPE: *Solandra grandiflora* Swartz. Figures 2B, 11.

Swartzia Gmelin, Systema naturae 2: 296, 390. 1791.
Solandra Kuntze, Rev. Gen. Plantarum. 452. 1891 (orthographic variant).

Woody lianas or high climbing epiphytic shrubs



Figure 11. *Solandra grandiflora* (Sims, J. 1817. Curtis's Botanical Magazine 44: t. 1874).

or small trees; stems glabrous or minutely pubescent, the trichomes glandular, simple or branched; bark shiny and loose, exfoliating when dry. Leaves elliptic, ovate or obovate, large and coriaceous, glabrous or pubescent with trichomes like those of the stems. Inflorescence terminal, a highly reduced cyme, usually with a single flower. Buds elongate, strongly exerted from the calyx tube, corolla aestivation quincuncial or cochlear. Pedicels at anthesis stout and woody. Flowers with the calyx 3–10 cm long, tubular, usually irregularly 2- to 5-lobed and zygomorphic, the lobes equal in length to the tube, occasionally somewhat purplish, glabrous or pubescent; corolla very large and showy, 13–40 cm long, zygomorphic, infundibuliform to cyathiform, white to cream or yellow, often with longitudinal purplish markings in the throat, darkening with age, the lobes rounded, entire to laciniate or fimbriate; filaments adnate to the corolla tube, exerted or included, declinate, densely pubescent at the point of insertion with simple, uniseriate trichomes; anthers basifixed, 6–

13 mm long, longitudinally dehiscent; pollen 3-colporate, coarsely reticulate; ovary 2-carpellate, 4-locular, glabrous, partially sunken into the receptacle and thus partly inferior; style equal in length to the filaments, glabrous, declinate, the stigma minute and capitate, bilobed. Fruit a leathery berry, conical, green or yellow when ripe, the calyx persistent and accrescent but splitting in fruit; seeds round or reniform, 4–6 × 2.5–4 mm, the cotyledons incumbent (fide Bernardello & Hunziker, 1987). 10 spp., West Indies, Mexico to the Amazon basin.

Literature. Bernardello & Hunziker (1987).

List of species. *Solandra brachycalyx* Kuntze, Costa Rica and Panama; **S. brevicalyx* Standl., NE Mexico; *S. boliviana* Britton, Bolivia; **S. grandiflora* Swartz, West Indies, Central and South America (*Datura sarmentosa* Lam., *D. scandens* Vellozo, *S. hirsuta* Dunal, *S. nitida* Zucc., *S. minor* Griseb., *S. scandens* (Vell.) Toledo, *Swartzia grandiflora* (Swartz) Gmelin); **S. guerrerensis* Martínez, Duran-

go, Mexico; **S. guttata* D. Don, Mexico; **S. longiflora* Tussac, West Indies, N South America (*S. laevis* Hooker, *S. macrantha* Dunal, *S. grandiflora* var. *macrantha* (Dunal) Voss); **S. maxima* (Sessé & Moçoiño) P. S. Green, Mexico, Central and N South America (*Datura maxima* Sessé & Moçoiño, *S. hartwegii* N. E. Brown, *S. selerae* Dammer); **S. nizandensis* Matuda, Mexico, Guatemala, Honduras; **S. paraensis* Ducke, Amazon basin in Colombia, French Guiana, Brazil.

The species of *Solandra* are widely cultivated for their showy flowers (Fig. 2B) in the tropics and subtropics throughout the world. These large yellowish flowers open in the evening, possibly suggesting bat pollination. Species in the genus are used by the Huichol and other groups in Mexico as hallucinogens (see references in Bernardello & Hunziker, 1987). The partially inferior ovary of *Solandra* is unique in Solanaceae. It is deeply sunk into the receptacle at anthesis, but specimens in fruit appear to be totally superior.

Solandra boliviana has often been considered to be a "linking" species between *Solandra* and *Schultesianthus* as it is superficially similar to the large-flowered *Sch. coriaceus*. Our results, however, demonstrate that *S. boliviana* shares not only gross morphological but also pollen synapomorphies with the rest of *Solandra* but not *Schultesianthus* (see Persson et al., 1994). The two genera are closely related (in our analysis sister groups, but in the analysis of Olmstead et al., in press, somewhat separate, see beginning of this article).

7. *Trianaea* Planch. & Linden, *Prix-Courant* 8: 4. 1853. TYPE: *Trianaea nobilis* Planch. & Linden. Figures 3B, 12.

Poortmannia Drake, *Bull. Soc. Philom. Paris*, ser. 8, 4: 128. 1892. TYPE: *Poortmannia speciosa* Drake.

Epiphytic or terrestrial shrubs or small trees, often clambering over other vegetation; stems flexuous, often dark purple when young; bark smooth or verrucose, glabrous to densely pubescent, gray or reddish brown. Leaves usually very large, 10–30 × 1–10 cm, narrowly linear to broadly elliptic, shiny and coriaceous, glabrous to minutely pubescent, densely hirsute in *T. naeka*, the trichomes simple and uniseriate. Buds elliptic, ± halfway exerted from the calyx tube, corolla aestivation quincuncial or cochlear. Pedicels at anthesis short and stout to long (ca. 5 cm) and pendant. Flowers with the calyx usually ± equal to the corolla tube at anthesis, somewhat inflated and strongly 5-angled, lobed ca. ½ way to the base, coriaceous, usually drying dark reddish brown or black, often somewhat purplish in



Figure 12. *Trianaea speciosa* (Drake) Soler. (Knapp et al. 9121, Loja–Zamora road, Ecuador), scale bar = 2 cm.

live plants, glabrous to minutely pubescent with simple uniseriate trichomes; corolla very large and fleshy, 5–15 cm long, broadly campanulate, green or greenish with purplish red markings on the throat, glabrous or densely pubescent without, the trichomes simple and uniseriate, the lobes triangular in outline, strongly reflexed at anthesis, the margins revolute; filaments adnate to the corolla tube in the lower ¼, usually strongly geniculate at the base, connivent around the straight style, glabrous along their entire length; anthers elongate, 1–1.5 cm long, usually white, ventrifixed, somewhat versatile; pollen 3-colporate, reticulate, with long, narrow colpi; ovary glabrous or minutely pubescent, style straight, glabrous, the stigma large, capitate to clavate. Fruit a berry, 3–6 cm long, 8–10-locular, green or purplish, the pericarp leathery, the pulp fleshy; seeds very small, 1–2 × 0.5–1 mm, reniform, but very thin, pale yellowish tan. About 6 spp., Colombia to N Peru.

List of species. *Trianaea brevipes* (Cuatr.) S. Knapp, Colombia and Ecuador (*T. spectabilis* Cuatr. var. *brevipes* Cuatr.); *T. naeka* S. Knapp, SE Ecuador, Cordillera del Condor; *T. neovisae* Romero-Cas-

tañeda, Sierra Nevada de Santa Marta, Colombia; *T. nobilis* Planch. & Linden, Colombia and Ecuador; *T. speciosa* (Drake) Soler., S Colombia to N Peru (*Poortmannia speciosa* Drake, *T. spectabilis* Cuatr.); *T. sp. nov.*, NC Peru, Cajamarca.

Trianaea is one of the most poorly collected genera in the Solanaceae. Its green flowers and position high in the canopy make it difficult to see and to access. The flowers of *Trianaea* are, like *Merinthopodium* and *Dyssochroma*, typical bat-pollinated flowers, and Vogel (1958) observed bats visiting the flowers of *T. brevipes* in Colombia. Persson et al. (1994) recognized two pollen types in the genus. However, although these show differences in the reticulum that enable them to be distinguished, they are very similar in overall pollen morphology.

The ovary of *Trianaea* is peculiar in Solanaceae in being 4–5-carpellate rather than the more typical 2-carpellate ovary found in the rest of the family (see Solereder, 1898, for a discussion). This character is difficult to see in flowering material, and as most specimens have a single flower, dissection is not desirable. Preserved collections are essential for the future study of this genus and its relationships to the rest of the green-flowered clade to which it belongs.

TAXA INCERTAE SEDIS

Markea lopezii Hunz., Cordillera Occidental, Colombia.—In the cladistic analysis this and a related species recognized but not named by Hunziker (1985) are the sister group of *Solandra*. The paucity of specimens for analysis and the fact that no fruiting specimens of *Markea lopezii* are known means this relationship needs further research. The pollen of *M. lopezii* is anomalous in the Juanulloeae (see Persson et al., 1994, and discussion above).

Several recent collections of epiphytic Solanaceae from Ecuador and adjacent Peru may certainly represent new taxa, and as more intensive collecting is done more specimens are likely to come to light.

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- Appendix. Selected Specimens Examined.
- Atropa belladonna* L.—Morocco: *Mohamed* 146 (BM).
- Lycium cestroides* Schlttdl.—Bolivia: *Fiebrig* 2213 (BM).
- Nicandra physaloides* (L.) Gaertner—Cultivated: *Higgins* 149 (BM).
- Dyssochroma longipes* (Sendtner) Miers—Brazil: *Sellow* 7769 (BM), *Lindeman & De Haas* 2543 (BM).
- Dyssochroma viridiflora* (Sims) Miers—Brazil: *Anon s.n.* (BM), *Mello Barreto* 1822 (K); *Pits* 1894 (K).
- Juanulloa ferruginea* Cuatrecasas—Peru: *Vásquez, Jaramillo, Arévalo & López* 4305 (NY), *Encarnación* 1285 (NY).
- Juanulloa globifera* (S. Knapp & D'Arcy) S. Knapp—Colombia: *Cogollo, Ramírez & Alvarez* 2895 (JAUM).
- Juanulloa membranacea* Rusby—Bolivia: *Britton & Rusby s.n.* (BM).
- Juanulloa mexicana* (Schlttdl.) Miers—Colombia: *Laurance s.n.* (BM); Costa Rica: *Anon s.n.* (BM); Mexico: *Cedillo & Calzada* 133 (BM).
- Juanulloa ochracea* Cuatrecasas—Colombia: *Schultes & Cabrera s.n.* (BM); Ecuador: *Baker & Trusher* 6118 (NY); Peru: *Ayala, Vásquez, Torres & Calderón s.n.* (NY), *Klug* 2360 (K).
- Juanulloa parasitica* Ruiz & Pavón—Bolivia: *Nee & Coimbra* 40085 (NY); Peru: *Foster* 9924 (NY), *Plowman & Schunke V.* 11765 (K).
- Juanulloa pavonii* (Miers) Benth. & Hook.—Ecuador: *Pavon s.n.* (BM), *Plowman & Alcorn* 14351 (NY); Peru: *Simpson & Schunke* 427 (NY).
- Juanulloa speciosa* (Miers) Dunal—Colombia: *Luteyn, Dumont & Buritica* 4884 (NY), *Anon s.n.* (BM).
- Juanulloa verrucosa* (Rusby) Hunz.—Bolivia: *Steinbach* 8466 (BM).
- Juanulloa wardiana* (D'Arcy) S. Knapp—Panama: *McDonagh, Lewis, Gumpel & Plumtre* 251 (BM), *Luteyn* 4096 (NY).
- Markea camponoti* Ducke—Brazil: *Daly, Campbell, Silva, da Silva, Bahia & dos Santos* D879 (NY), *Guèdes s.n.* (BM); Guyana: *Bartlett* 5414 (K).
- Markea coccinea* L. C. Richard—Brazil: *Egler* 47679 (NY), *Mori, Mora Cardoso, deSilva & Sothers* 20215 (NY); Colombia: *Schultes & Cabrera s.n.* (BM); Guyana: *Myers* 5953 (K); Peru: *Foster, Fernández & Vivar* 10766 (NY).
- Markea costanensis* Steyerem.—Venezuela: *Steyermark & Davidse* 116312 (NY), *Steyermark & Davidse* 116951 (NY).
- Markea formicarum* Ducke—Peru: *Ayala, Vásquez, Torres & Calderón* 2563 (NY); Venezuela: *Nee* 30923 (NY).
- Markea lopezii* Hunz.—Colombia: *Croat* 50164 (MO), *Gentry, Juncosa & Gomez* 40820 (NY).
- Markea panamensis* Standl.—Colombia: *Forero, Jaramillo & Lean* 1606 (NY); Panama: *de Nevers, Herrera & Charnley* 5041 (K), *Gentry* 8761 (NY), *Kirkbride & Briston* 1454 (NY), *McDonagh, Lewis, Gumpel & Plumtre* 101 (BM).
- Markea sessiliflora* Ducke—Guyana: *Anon* 3974 (K), *Jenman* 633 (K), *Pipoly* 7556 (NY); Brazil: *Ducke s.n.* (BM).
- Markea ulei* (Dammer) Cuatr.—Peru: *Vásquez & Jaramillo* 9647 (NY), *Ramos & Lima* 17170 (NY).
- Merinthopodium neuranthum* (Hemsl.) Donn. Sm.—Belize: *Hazlett & Coe* 2748 (NY), *Peck* 508 (NY); Colombia: *Sánchez, Orrego, Sylva, Martinez, Restrepo & Bahamon* 1559 (NY); Costa Rica: *Wilbur & Stone* 10091 (NY); Nicaragua: *Gomez* 21033 (MO), *Moreno* 23392 (MO); *Stevens & Krukoff s.n.* (BM); Panama: *Hammel* 6096 (NY), *McPherson & Aranda* 10175 (BM); Venezuela: *Luteyn, Lebron-Luteyn, Ruíz-Terán & Dugarte* 5354 (BM).
- Schultesianthus coriaceus* (Kuntze) Hunz.—Colombia: *Nee & Callejas* 32545 (NY), *Tracey s.n.* (K), *Zarucchi, Brant & Betancour* 6034 (NY).
- Schultesianthus crosbianus* (D'Arcy) S. Knapp—Costa Rica: *Davidse, Herrera & Grayum* 28688 (NY); Panama: *Folsom, Channell, Dressler & Dressler* 7117 (MO), *de Nevers & Charnley* 6058 (BM).
- Schultesianthus dudleyi* Bernardello & Hunz.—Ecuador: *Madsen* 86180 (NY), *Madsen & Elleman* 75160 (BM).
- Schultesianthus leucanthus* (Donn. Sm.) Hunz.—Panama: *Hampshire & Whitefoord* 469 (BM).
- Schultesianthus megalandrus* (Dunal) Hunz.—Costa Rica: *Haber & Cruz* 8402 (BM), *Herrera* 502 (BM); Venezuela: *Steyermark & Steyermark* 9529 (K).
- Schultesianthus uniflorus* (Lundell) S. Knapp—Mexico: *Breedlove & Smith* 31710 (MO).
- Schultesianthus venosus* (Standley & C. V. Morton) S. Knapp—Costa Rica: *Grayum, Haufler & Rous* 7755 (NY); Panama: *Hampshire & Whitefoord* 856 (BM).
- Solandra boliviana* Britton—Bolivia: *Gentry & Solomon* 52048 (NY), *Croat* 51550 (MO).
- Solandra brachycalyx* Kuntze—Costa Rica: *Lankester s.n.* (K); Panama: *Hammel* 7360 (BM).
- Trianaea brevipes* (Cuatr.) S. Knapp—Ecuador: *Palacios & van der Werff* 3673 (NY).
- Trianaea naeka* S. Knapp—Ecuador: *Neill & Cerón* 7449 (NY).

Trianaea neovisae Romero-Castañeda—Peru: Díaz & Osores 2944 (MO).

Trianaea nobilis Planch. & Linden—Colombia: Silverstone-Sopkin 1188 (MO); Ecuador: Zak 1028 (K).

Trianaea speciosa (Drake) Soler.—Ecuador: Boeke 547

(NY), Gentry, Bonifaz & Looor 30950 (MO), Dodson & Dodson 18592 (NY); Spruce 5527 (K); Peru: Barbour 4113 (MO).

Trianaea sp. nov.—Peru: Díaz, Osores & Bustamente 3935 (MO).